Chimpanzees of Gabon and Chimpanzees of Gombe : some comparative data on the diet

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Chimpanzees of Gabon and Chimpanzees of Gombe: some Comparative Data on the Diet

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1. INTRODUCTION

The feeding behaviour and diet of chimpanzees in Gabon (*Pan troglodytes troglodytes*), was the subject of a one-year field study in 1971–72 (Hladik,

FIG. 1. Inside the rain forest at Ipassa.

1973). A parallel study of feeding behaviour on the well known population of *Pan troglodytes schweinfurthii* in the Gombe National Park, was carried out in 1972–73 (Wrangham, 1975 and this volume). Unfortunately, the scope of the comparison of these two studies is limited by the small amount of information concerning diet (quantification and composition) available for the latter population.

2. METHODS

2.1. Comparison of Study Areas

The Gabon study was carried out at the CNRS field station of Ipassa (500 m), mainly on a 2-km-long island in the Ivindo river. Vegetation diversity in the study area is very high and over 900 plant species have been determined and listed (Hladik and Hallé, 1973). Many lianas (Fig. 1) play an important part in the production of this forest (A. Hladik, 1974), especially in fruit production. The chimpanzee population consisted of eight subadults introduced into the island from the nearby forest. The chimpanzees were well habituated and the observer could usually stand among the group when recording. Bananas were provided at an artificial feeding area and, except during the minor dry season (when the fruits were very abundant), the animals obtained about 30% of their food from this. The observations were resumed in the 1975 minor dry season and little food was provided, the animals feeding on natural fruits, particularly those of *Irvingia gabonensis*.

In contrast, the habitat at Gombe is drier and more mountainous (Goodall, 1965; Clutton-Brock, 1975a). It includes open woodland and grassland and the vegetation is less diverse (see Clutton-Brock, 1975a; Appendix II: at Gombe only nine species account for 50% of the tree population, while in the Ipassa forest, in a smaller sample, 15 species accounted for 50% of the tree population).

At Gombe, the chimpanzees obtained small amounts of bananas from the artificial feeding area (less than 20% of their food, according to Wrangham), but were not fed during Wrangham's study.

2.2. Field Methods

Individual animals were observed from dawn to dusk and their food intake recorded using the methodology described in Chapter 11. As Table I shows, the amount of time spent feeding on different foods was not closely related to their abundance in the diet.

Food samples were collected in order to calculate the weight of the

TABLE I

Comparison between the time spent feeding and the food intake by Pan troglodytes troglodytes

Sample eaten	Time spent			Amount ingested fresh weight		
	min	%		g	%	
Baphia leptobotrys (Papilionaceae) leaves	35	16·7	48·8% of the feeding time spent on leaves and bark	85	5·3	33·3% of the fresh weight ingested from leaves and bark
Hypselodelphis violacea (Marantaceae) stems	12	5·7		120	7·5	
Musanga cecropioides (Moraceae) petioles of leaves	2	0·9		10	0·6	
bark	3	1·4		30	1·9	
Pterygota bequaertii (Sterculiaceae) young leaves	12	5·7		135	8·5	
stems	3	1·4		10	0·6	
Macaranga spinosa (Euphorbiaceae) bark	3	1·4		15	0·9	
Roureopsis obliquifoliolata (Connaraceae) leaves	9	4·3		50	3·1	
Baphia sp. 1383 (Papilionaceae) leaves	4	1·9		5	0·3	
Vine (unidentified) apex	8	3·8		20	1·3	
Musa sapientum (Musaceae) banana skins	11	5·3		50	3·1	
Garcinia polyantha (Guttiferae) pulp of fruits	8	3·8	14·4% on fruits	15	0·9	62·6% from fruits
Mammea africana (Guttiferae) pulp of fruits	6	2·9		50	3·1	
Cissus dinklagei (Vitaceae) fruits	2	0·9		10	0·6	
Musa sapientum (Musaceae) banana pulp	14	6·7		920	57·9	
Macromiscoides aculeatus ant nests	64	30·6	36·8% on insects	45	2·8	4·1% from insects
Termites (including rotten wood)	4	1·9		15	0·9	
Ants (unidentified)	9	4·3		±5	0·3	

Example of 1st September 1971, from 5.40 to 18.07h.

food ingested by the chimpanzees (average fresh weight). They were preserved by boiling in alcohol or by drying in an electric oven (see Appendix III this volume).

2.3. Observation Sample

In Gabon, total observation time was 27 090 minutes during the 1971–72 field study. The dots along the time-axis of Fig. 4 indicate the days during which continuous observations were made.

3. COMPARATIVE ASPECTS OF FEEDING BEHAVIOUR

3.1. Daily Variation in Food Intake

As in other areas where they have been studied (Goodall, 1963, 1965; Reynolds and Reynolds, 1965; Suzuki, 1969; Jones and Sabater Pi, 1971) the chimpanzees at Ipassa were primarily frugivorous. During the observation sample of 1971–72, 141 plant food types (plus 33 animal foods and five mineral foods) were identified and a further 144 (accounting for small amounts ingested) could not be identified. This suggests that the chimpanzees ate a higher number of food types than in Gombe, where Wrangham (this volume) recorded that they ate 140 food types during an observation sample twice as long as ours. This is supported by comparison of the average number of food types eaten per day: more than 20 at Ipassa versus 14·6 at Gombe. In contrast, the numbers of feeding bouts per day were similar in the two areas. Teleki (pers. comm.) suggested that the differences in the number of foods selected between the two areas could be related to the differences in the age classes observed.

Although this may be a contributory factor, the greater number of edible species available in Gabon, must also be involved.

Different foods tend to be eaten at different times of day (Fig. 2) and this pattern varies seasonally. During the minor dry season, fruits are eaten at the beginning and at the end of the day, while leaves tend to be eaten most during the middle of the day, following the main period of fruit-eating. In the rainy season, fruits are eaten throughout the day (generally because they are found in small amounts dispersed across the range) and leaf-eating shows a marked peak in the late afternoon. The species from which leaves and stems are eaten, are generally abundant and can be found easily in the different parts of the range, and the diurnal rhythm in food choice is not a product of the occasional finding of different plant species. Wrangham (this volume, Fig. 8) found a

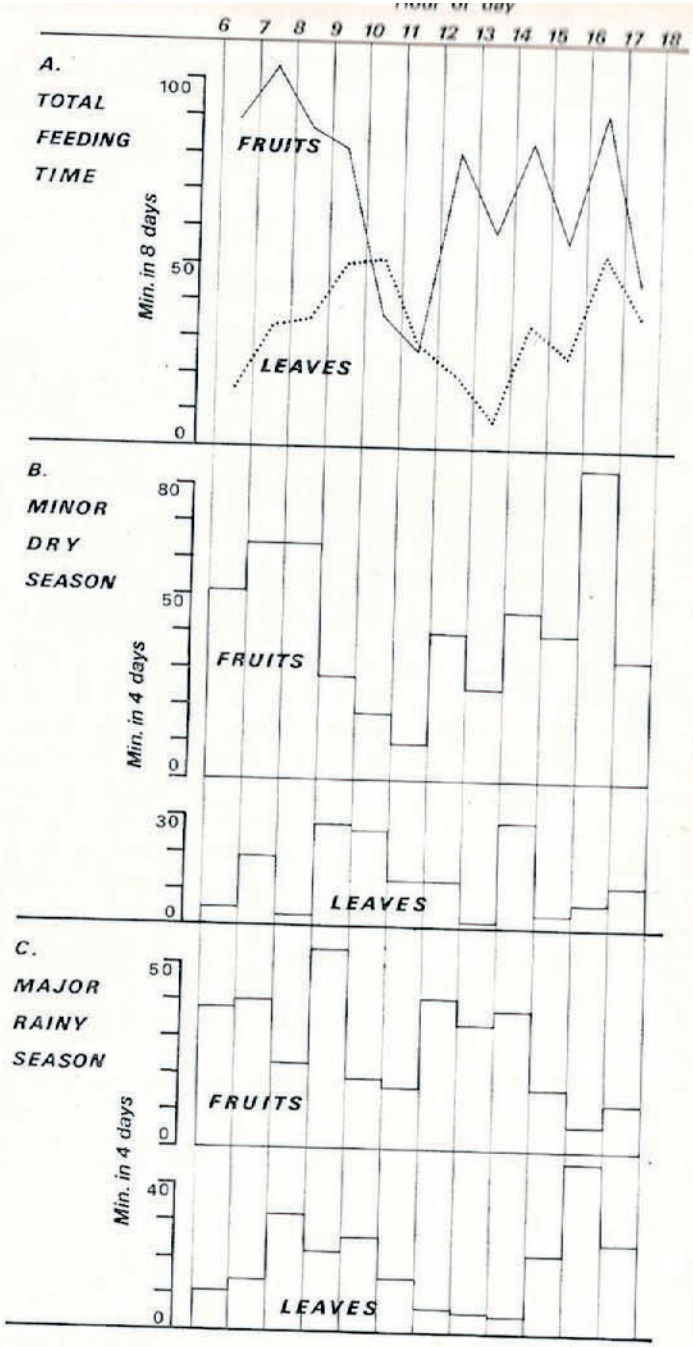

FIG. 2. Diurnal variation in time spent feeding on fruits and leaves by *Pan troglodytes troglodytes*, in Gabon.

similar difference between the times when leaves and fruits were eaten at Gombe.

3.2. Feeding Techniques and Traditions

Some differences in feeding behaviour between the chimpanzees in Gabon and at Gombe are noticeable (Hladik, 1973) and the main points of comparison are related to tool-using.

Feeding on ants and termites is important to maintain the protein balance of the diet of the chimpanzee (see Section 5.2). Several ant species including *Macromiscoïdes aculeatus*, *Oecophylla longinoda*, *Polyrhachis militaris*, *Paltothyreus tarsatus* and *Camponotus* sp. are eaten, many of them after "fishing", a technique similar to that described for termite-eating at Gombe (Goodall, 1968), using a stem from which leaves have been stripped off with the mouth. At Gombe, *Macrotermes bellicosus* are caught with a grass stem (McGrew, 1974) while *Macrotermes muellerii*, although obviously edible, are not eaten by the chimpanzees in Gabon.

In contrast, feeding on scorpions was only observed in Gabon. At least one species, *Opisthacanthus lecomtei*, was killed by a rapid hand-slap before being chewed with some pieces of bark.

The bark from different trees and lianas is utilized by the chimpanzees in Gabon and chewed with any kind of animal food such as eggs and fledglings. At Gombe, some leaves are utilized for the same purpose. In addition, leaves that are never taken as food are also chewed to make "sponges" to extract the brain of prey (Teleki, 1973a) or to clean out the inside of hard-shelled fruits (Wrangham, this volume). The fibre wad although made by the chimpanzees in Gabon, was never actually made intentionally, as it was at Gombe. It was generally made from the stems of *Hypselodelphis violacea*, which was frequently eaten throughout the year (Fig. 3): the fibre, generally spat out, can be used as a sponge to drink water in a hole of a tree trunk.

Nut breaking with a tool was observed neither in Gabon nor at Gombe. In places where *Panda oleosa* and *Coula edulis* are eaten by the chimpanzees after breaking the hard shell of the nut (Struhsaker and Hunkeler, 1971; Rahm, 1971), there are obvious traces which have never been observed in Gabon, in spite of the abundance of *Panda* and *Coula*.

4. VARIATION IN FEEDING AND RANGING BEHAVIOUR

4.1. Seasonal Variation

Changes of the relative proportions of the fresh weight of fruits and leaves ingested (Fig. 4) can be related to the seasonal changes below.

FIG. 3. A subadult female chimpanzee peeling, before chewing, the stem of a Marantaceae: *Hypselodelphis violacea*.

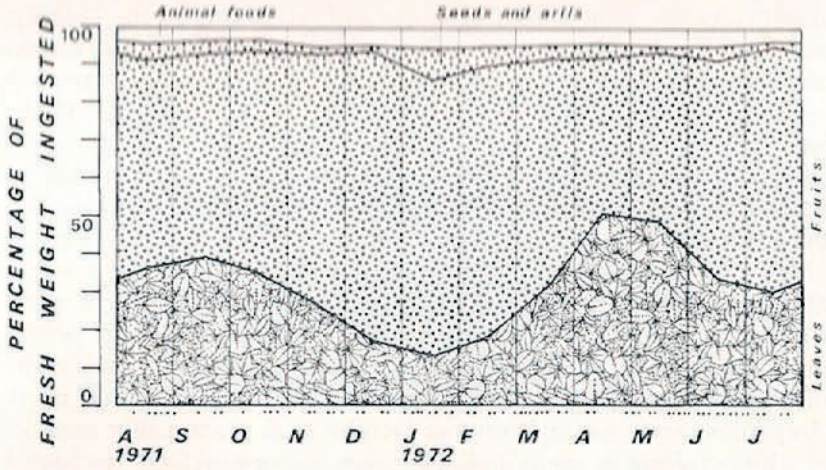

FIG. 4. Percentages of fresh weight of different food categories ingested by the chimpanzee in Gabon and their variation throughout the year. Young and mature leaves and stems are all included in the same category (bottom of the graph).

(a) During the major dry season (approx. July–Sept.) in Gabon, few fruit species are available. Consequently, the leaves and stems of some common species are eaten in large proportions (up to 40% of the diet).

(b) During the major rainy season that follows (Oct.–Dec.), many species start fruiting and the proportion of leaves included in the diet decreases as soon as the fruits are eaten in large amounts.

(c) A maximum of fruits is available during the minor dry season (Jan.–March). Very few leaves and stems (15% of the diet) are eaten in January but the proportion increases rapidly and the diet includes many young leaves and shoots available at this time.

(d) During the minor rainy season (April–June), when fruits are less abundant, the proportion of leaves and shoots in the diet reaches the maximum of 50%.

Animal foods are eaten in small amounts (4%) throughout the year. The mature or immature seeds of a few species are also eaten (more than 5%) when they are available.

The progressive variation in the gross food categories included in the diet of the chimpanzee in Gabon is the result of the addition of a large number of food species (see Hladik, 1973, fig. 13). No one species accounts for a large proportion of the annual diet.

At Gombe, according to Wrangham (Fig. 7, this volume), a similar pattern of annual variation of the diet results from the utilization of a smaller number of food species but one of these species, *Elaeis guineensis*,

accounts for the bulk of feeding time (and, according to the high lipid content of *Elaeis* fruits, this must also be the bulk of the diet in terms of calories). In the rainy season, the leaves of two species (*Pterocarpus tinctorius* and *Baphia capparidifolia*) account for about 25% of the feeding time, while in Gabon at the same time, the leaves and stems of four species (*Baphia leptobotrys*, *Hypselodelphis violacea*, *Pterygota bequaertii* and *Newbouldia laevis*) account for 30% of the food intake with about 20 other species being eaten in small amount.

Many trees in the rain forest present an irregular phenological pattern (A. Hladik, 1977) and there are important differences of production between successive years (for example, the average production of fruits during the 1972 minor dry season was half that of the 1975 minor dry season). The resulting differences in the diet of the chimpanzees seem as important at Gombe as in Gabon. For instance, the fruits of *Parinari curatellifolia* were an important food resource in 1973, at Gombe (41% of the feeding time during the fruiting period) but were not available in 1972. Similarly, in Gabon, the fruits of *Irvingia gabonensis* were extremely abundant in 1975 (more than 50% of the food ingested in the records of February) but no fruiting occurred in 1972. Nevertheless, the general pattern of the diet was very similar in 1972 and 1975.

4.2. Annual Food Intake

Figure 5 shows the average proportions of the different foods eaten by the chimpanzees in Gabon during one year, in terms of fresh weight: 68% of fruits; 28% of leaves and stems; 4% of animal food (insects and small prey) plus a very small amount of earth ingested.

Variations in the proportions of the different foods eaten each day is illustrated by the hatched columns indicating the maximum and the minimum observed. Fruits may form up to 90% of the daily intake and never less than 40%, but most of the daily records include between 55 and 80% of fruits. The daily intake of animal food (essentially the ants, some termites, bird eggs and fledglings) varies between 2·5 and 6%.

A comparison with Gombe is difficult in terms of food intake. The similar seasonal variation in feeding times cannot be applied to food intake, as shown in Section 2.2. The feeding time on leaves is shorter at Gombe than in Gabon and the proportion eaten may be smaller. On the other hand, the chimpanzees at Gombe eat small-sized game (Teleki, 1973a, 1975) and adult males spend a long time interacting and sharing the meat. The average consumption is around 10 g of meat per

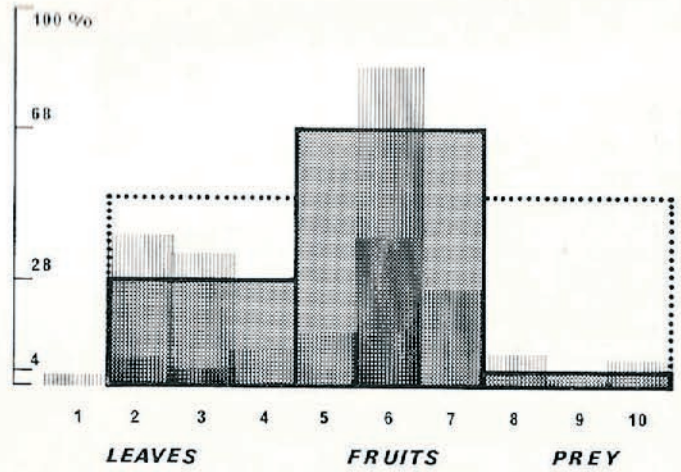

FIG. 5. Relative proportions of different food categories in the annual food intake of the chimpanzee in Gabon. The three shaded areas represent leaves (28%), fruits (68%) and animal foods (4%).

Maxima and minima of daily food intake are shown by the hatched columns for earth (1); bark and stems (2); leaves, shoots and pith (3); flower buds and gums (4); immature fruits (5); ripe fruits (6); seeds and arils (7); small arthropods (8); large arthropods (9) and eggs and fledglings (10).

day per chimpanzee (Wrangham, pers. comm.) and, as a dietary protein complement, is of little importance (less than 0·5% of the diet) compared with the other types of animal foods, especially ants and termites.

4.3. Ranging Patterns

The distance travelled each day by the subadult female chimpanzees observed in Gabon was smaller than in Gombe, but on the small island where they have been observed, the physical limits may have restricted ranging patterns. The subgroupings and some other sociological factors of the history of the group (see C. M. Hladik, 1974) were partly related to the direction of travel, but movements were also influenced by the distribution of food.

Foraging was more frequent in the mid-canopy than on the ground. They had some preferred nesting places in tall trees (40–50 m) but none of these sites were ever occupied on two consecutive nights.

TABLE II

Composition of some important food samples eaten by the chimpanzee in Gabon

	Water (%)	Per cent of dry weight								
		Protein	Lipids	Sugars after hydrol.	Cellulose	Minerals	Phosphorus	Calcium	Chlorides in NaCl	Potassium
FRUITS										
Nauclea diderrichii (Rubiaceae) seeds not extracted	76·7	4·5	5·3	47·2	17·3	3·0	0·11	0·27	0·10	0·97
Duboscia macrocarpa (Tiliaceae)	68·0	4·2	1·8	44·8	35·0	3·1	0·09	0·32	0·06	0·97
Aframomum giganteum (Zingiberaceae) seeds not extracted	55·9	8·2	11·1	48·8	11·6	5·2	0·18	0·10	0·13	1·68
Musanga cecropioides (Moraceae) seeds not extracted	72·8	8·8	6·3	31·5	25·9	4·5	0·17	0·67	0·19	1·19
Sarcophrynium schweinfurthianum (Marantaceae) seeds not extracted	61·8	11·3	0·9	61·8	14·6	4·7	0·19	0·66	0·13	0·85
Mammea africana (Guttiferae)	81·1	5·1	—	—	10·6	2·7	0·09	0·17	—	0·69
Pseudospondias longifolia (Anacardiaceae)	73·7	7·5	0·6	17·4	28·8	14·0	0·07	0·23	0·19	1·83
Rytigynia sp. 2032 (Rubiaceae)	84·9	8·1	5·9	8·6	27·6	3·5	0·07	0·13	0·10	1·18
Musa sapientnm (Musaceae) banana pulp	69·1	4·5	1·2	84·7	1·7	3·8	0·11	0·14	0·32	1·28
with skin	78·4	5·6	6·6	42·0	8·6	7·8	0·16	0·61	0·44	2·73
SEEDS AND ARILS										
Dichostemma glaucescens (Euphorbiaceae) unripe seeds	88·9	10·1	0·8	37·7	15·0	2·4	0·14	0·17	0·19	0·83
Cryptosepalum congolanum (Caesalpiniaceae)	67·1	10·6	3·0	7·0	2·4	2·3	0·20	0·15	0·13	0·75
Oubanguia africana (Scytopetalaceae) unripe seeds	68·8	7·0	0·4	—	4·5	2·8	0·14	0·22	0·35	0·47
Treculia africana (Moraceae) seeds	18·2	13·3	11·9	74·0	1·9	11·9	0·25	0·11	0·26	1·17
Trichilia prieureana (Meliaceae) arils	46·2	11·5	73·2	5·6	5·3	1·6	0·12	0·13	0·06	0·46
FLOWERS										
Neuropeltis acuminata (Convolvulaceae)	68·8	25·4	1·8	16·7	19·2	6·8	0·28	0·45	0·28	2·47
Cryptosepalum congolanum (Caesalpiniaceae)	65·0	18·5	1·7	—	12·5	4·9	0·30	0·24	0·10	1·39
LEAVES AND STEMS										
Baphia leptobotrys (Papilionaceae) leaf buds	80·7	55·0	—	—	12·3	6·4	0·69	0·49	—	1·28
young leaves	74·3	36·3	2·3	20·1	14·9	3·7	0·20	0·27	0·06	1·18
large leaves	59·0	31·9	1·9	11·4	28·0	11·1	0·12	1·75	0·13	1·77
old leaves	56·7	26·1	1·3	—	36·6	8·9	0·19	1·14	—	1·26
Newbouldia laevis (Bignoniaceae) young leaves	76·6	21·7	4·1	—	13·8	5·4	0·28	0·22	—	1·91
Dinophora spenneroides (Melastomaceae) young leaves	83·6	16·7	10·7	31·2	11·0	3·6	0·20	0·46	0·15	1·72
Ongokea gore (Olacaceae) young leaves	66·3	19·3	1·2	25·0	8·9	3·9	0·22	0·22	—	1·21
Baphia sp. 1383 (Papilionaceae) young leaves	67·5	24·5	1·3	14·5	37·0	4·1	0·22	0·19	0·16	1·42
Hypselodelphis violacea (Marantaceae) stems	74·1	5·7	1·1	11·4	51·3	4·9	0·10	0·22	0·50	1·38
Musanga cecropioides (Moraceae) petiolcs	91·7	11·6	0·6	17·0	19·3	17·1	0·26	2·40	1·34	5·44
INVERTEBRATES										
Macromiscoides aculeatus total ant nests	±50	29·0	4·2	20·0	—	5·0	0·36	0·61	—	—
Œcophilla loginada ant grubs	—	71·5	—	—	—	—	—	—	—	—
Mixture of insects from the litter	—	70·2	3·5	0·5	—	6·1	0·76	0·70	—	—
Caterpillars, sample An 15	72·9	62·3	21·2	6·4	7·3	3·2	0·39	0·21	0·19	1·11

5. FOOD COMPOSITION

5.1. Variability Among Food Categories

The results of the analysis of food samples collected in Gabon (Table II) show the necessity of combining different food categories to obtain a balanced diet. Protein content of fruits is generally low: the sample average (6·8%) is biased by the presence of fruits with small seeds (seeds are broken during the process of homogenization preceding analysis but usually found intact in the animals' faeces). Thus, in the pulp of most of the fruits, there is no more than 5% protein, which is insufficient to compensate for the loss of nitrogen of an adult chimpanzee. Seeds and arils are not rich enough (average 10·5% protein) to complement the fruits and not available in sufficient amount. By contrast, leaves and stems are common and have a high protein content (average of 24·9% for the ten samples). These, especially young leaves and shoots, may be eaten to complement fruit when invertebrates or the other animal prey cannot be obtained in sufficient quantity. A further ecological analysis of the relation of the food types with body mass and food availability is presented in C. M. Hladik (1977).

A rapid review of the other components listed in Table II indicates that only a mixture of the different food categories can give a balanced diet. Energy is found in the lipids of seeds and arils and in the glucids of the fruits (a technique of weak hydrolysis shows in terms of sugars what would be available as nutrients).

The proportion of different minerals varies between the different samples and only the combination of many plant species can result in a constant and balanced average. Phosphorus must be partly taken from animal foods while calcium is abundant in most leaf specimens. Some vegetable food, especially *Hypselodelphis violacea* stems and the petioles of *Musanga cecropioides* are extremely poor in nutrients: their selection by the chimpanzee is presumably related to their exceptionally high mineral content.

5.2. Protein Intake

Why are invertebrates eaten by chimpanzees? Leaves, which can be collected and eaten in a relatively short time, yield more protein than the small amounts of insects for which the chimpanzees foraged for 30–50% of the feeding time. One explanation may be the lower digestibility of plant protein when the proportion of fibre is high in the

TABLE III

Comparison of the relative proportions of the essential amino acids in the vegetal and animal food samples accounting for most of the dietary protein ingested by the chimpanzee, Pan troglodytes troglodytes *in the forest of Gabon*

Amino acid	Stems of *Hypselodelphis violacea*	Leaves of *Baphia leptobotrys*	Ants nest of *Macromiscoides aculeatus*	Ants and grubs of *Œcophylla longinoda*	Total average	Protein of egg as reference
Cystine	4·6	7·7	2·7	1·75	5·9	4·8
Histidine	4·8	2·9	9·0	6·6	4·3	4·6
Isoleucine	11·0	11·5	11·3	12·4	11·6	10·4
Leucine	20·3	13·5	19·2	22·1	16·2	16·7
Lysine	10·5	8·7	12·9	15·0	10·4	13·9
Methionine	4·6	2·7	3·4	3·5	3·1	6·1
Phenylalanine	11·5	8·7	8·1	7·6	8·7	11·6
Threonine	11·8	7·9	11·3	10·2	9·0	9·3
Tyrosine	6·1	9·0	8·7	8·4	8·6	9·3
Valine	15·2	27·6	13·4	12·4	22·3	13·5

The percentages of essential amino acids are related to their sum. The "total average" is calculated according to the importance of each sample in the diet of the chimpanzee. From Hladik and Viroben, 1974.

sample. In addition, insects may be eaten to supply essential amino acids, not present in sufficient amounts in plants. In Gabon, the chimpanzee utilizes relatively few plant species in large quantities: during the rainy season, most of the leaves and stems are taken from four species (see Section 4.1) and two of them are eaten throughout the year (*Hypselodelphis* and *Baphia* leaves). It is noticeable that the amino acids of these two plants are partly complementary: the leaves of *Baphia* contain little leucine and threonine, while the shoots and stems of *Hypselodelphis* have a larger proportion of these amino acids in their protein (Table III). Nevertheless, the average proportions of histidine, leucine, lysine and threonine are low, due to an excess of valine. The ants eaten throughout the year (*Macromiscoïdes* and *Oecophylla*) compensate this lack of some essential amino acids. Conversely, feeding solely on insects would result in a lack of cystine (Hladik and Viroben, 1974).

The termites eaten at Gombe by the chimpanzees probably play the same role as the ants in Gabon and complement the proteins obtained from leaves. The composition of the protein fraction of *Macrotermes bellicosus* (Table IV) is fairly similar to that of the ants, with a percentage of phenylalanine and, to a lesser extent, of methionine, closer to the ideal proportions of egg protein used for comparison.

Among the termites of the above species, reproductives and soldiers

TABLE IV

Results of the analysis of the protein fraction of a sample of reproductive Macrotermes bellicosus *collected at Gombe by R. W. Wrangham*

Protein	% of total protein	% of essential amino acids
Aspartic acid	7·6	
Threonine	3·7	9·1
Serine	3·4	
Glutamic acid	10·0	
Proline	4·8	
Glycine	4·8	
Alanine	5·9	
Valine	5·1	12·6
Isoleucine	3·8	9·5
Leucine	6·8	16·9
Tyrosine	6·3	15·7
Phenylalanine	4·1	10·1
Lysine	5·6	13·9
Histidine	2·7	6·6
Arginine	5·1	
Methionine	1·6	4·0
Cystine	0·7	1·6

TABLE V

Comparison of protein content of different samples of Macrotermes bellicosus *collected at Gombe by R. W. Wrangham*

	Per cent of dry weight		
	Protein (N × 6·25)	Lipids	Glucids after hydrolysis
Reproductives (eaten)	40·6	52·8	—
Soldiers (eaten)	58·7	<35	—
Workers (not eaten)	68·4	<25	2·1

but not workers are eaten by the chimpanzees. Curiously, analysis of the samples collected in Gombe by Wrangham, indicates that workers yield the maximum amount of protein (Table V). Selection of termites as food may be related mainly to the lipid content (detected by taste). Reproductives yield 52·8% lipids, while in the workers lipids account for less than 25%. The unsaturated fatty acids found in animal lipids may be as important in the diet as the amino acids.

In Gabon, scorpions, of which the hepatopancreas and haemolymph are the main edible parts, are often eaten. Haemolymph is poor in fat but rich in free amino acids (M. Goyffon, pers. comm.) while glycogen and phospholipids are important components of the hepatopancreas. It is likely that the grouping of several of those components are responsible for the attractiveness of these arachnids.

5.3. Mineral Intake

Geophagy is common in chimpanzees, both in Gabon and at Gombe. Up to twice a day, animals ate pieces of earth of about 10 to 20 g. The different earth samples are described in Hladik (1973). All of them are made of clay or other phyllitous materials with particules smaller than 2 μm and most of them from earth that has been moulded by insects (very soft and with fine structure). The cylindric constructions ("chimneys") built by the larvae of *Muansa clypealis* (Homoptera) were often eaten by all the chimpanzees of the group.

The mineral content of these specimens of earth (Table VI) does not reveal any element in sufficient concentration to interact with mineral nutrition (Hladik and Gueguen, 1974). This was also the case of the earth samples eaten by the *Presbytis* species in Sri Lanka (see Hladik, this volume) and by other primates, mostly leaf-eaters, for which analytical data are available. The elements which might have some nutritive value for the chimpanzees occur at lower levels in the earth

TABLE VI

Mineral content of different earth samples eaten by the chimpanzee, Pan troglodytes troglodytes, *in Gabon*

	P	Ca	Mg	K	Na	Fe	Zn	Mn	Cu
Earth from cylindric construction of *Muansa clypealis* larvae	94	114	100	440	104	8600	21	18	8
Earth from mounds of *Macrotermes muellerii*	10	94	—	182	4	—	—	—	—
Earth sample collected near the above mounds	10	8	—	100	5	—	—	—	—
Earth from dripping part of the nest of *Procubitermes* sp.	490	448	70	540	95	33 000	35	54	14

The proportions of the different elements are in 10^{-6} (millionth of the dry weight). After Hladik and Gueguen, 1974.

samples than in many common food plants (Table VII). The low levels of some minerals in the diet are compensated by feeding on a few species with a high mineral content, such as the stems of *Hypselodelphis violacea* and particularly the petioles of *Musanga cecropioides* which contain $13\,380 \times 10^{-6}$ of chlorides. A similar example of adaptation to mineral nutrition is presented by Oates (1974 and this volume): a *Colobus* monkey obtained most of its sodium from *Hydrocotyle ranunculoides*, a plant occurring only in a swamp. The situation at Gombe seems quite similar. The composition of the earth samples ingested by the chimpanzees (Table VIII) differs only in the larger amounts of calcium and potassium.

The most likely function of eating clay and other phyllitous material is that it acts as an adsorbant of certain components of the stomach content such as tannins (C. M. Hladik, 1977 and this volume).

TABLE VII

Mineral content of some food samples eaten by the chimpanzee, Pan troglodytes troglodytes, *in Gabon*

	P	Ca	K
Baphia leptobotrys, young leaves	1990	2660	11 790
mature leaves	2510	3690	16 140
Hypselodelphis violacea, stems	990	2180	13 790
Nauclea diderrichii, fruits	1090	2680	9650
Musanga cecropioides, petioles of leaves	2620	23 970	54 440

The proportions of the different elements are in 10^{-6} (millionth of the dry weight).

TABLE VIII

Mineral content of samples of the earth eaten by the chimpanzee, Pan troglodytes schweinfurthii, *at Gombe (Tanzania), collected by R. W. Wrangham*

	Ca	Mg	K	Na	Zn	Mn	Cu
Termite mound of *Macrotermes bellicosus*							
sample RW 1	600	600	5490	210	23	137	24
sample RW 2	580	4200	4580	130	20	96	19

The proportions of the different elements are in 10^{-6} (millionth of the dry weight).

5.4. Secondary Compounds

Tannins, alkaloids, saponines, terpenes and other secondary compounds are found in small quantities in many plant species and in large amounts in a few species. Where they are very abundant, some parts of the plant may be toxic and inedible.

Chimpanzees, like many other primates, are unable to detoxify substances by a fermentation preceding absorption and might be poisoned if the toxic substance is ingested. Thirty-eight foods eaten by the chimpanzees in Gabon were tested for alkaloids with Mayer and Dragendorff reagents. Testing was restricted to the foods (leaves and seeds) in which alkaloids were likely to occur. Similar tests were also carried out on a sample of 382 plant species collected at random in the rain forest of Ipassa where the chimpanzees have been observed (A. Hladik, 1977). In both samples, around 15% of species gave positive results indicating that the chimpanzees showed little selection against plants containing alkaloids. The main conclusion is that the alkaloids, in most of the plants in which they occur, are not toxic or not concentrated enough to be toxic. By contrast, a few species with a high alkaloid content such as the fruit of *Picralima nitida* (Apocynaceae) are not eaten by the chimpanzees.

Saponines, steroids and terpenes were found by Bouquet (1972, 1975) in a few species of the Congo rain forest, which also occur in Gabon and are eaten by the chimpanzees; but only tannins occur frequently in the leaves and bark of many species and are likely to interact with feeding behaviour (see discussion about leaf-monkeys, Hladik, this volume). In the bananas eaten by the chimpanzees at Gombe (and also frequently eaten in the old plantations in Gabon) some 3,4 dihydroxyphenylalanine (Waalkes *et al.*, 1958) may be concentrated in the skin (700×10^{-6}) which is chewed with the pulp without any apparent effect.

6. CONCLUSION

The study suggested that food choice in the chimpanzees was affected by variation in the levels of specific nutrients in different foods rather than by variation in secondary compounds. Several points supported this view. When the chimpanzees did not appear to be maximizing their energy return they compensated for deficiencies in the qualitative composition of their diet by ingesting species yielding specific nutrients. For example, they ate the tiny leaf buds of *Baphia leptobotrys*, weighing 0·05 g each and the rate of ingestion when feeding on these parts was evidently slow. This item is of great importance for it provides certain amino acids. Similarly, when the chimpanzees ate the petioles of *Musanga cecropioides*, which yield mostly fibre as a primary component, this helped to balance the mineral content of the diet.

The feeding strategy of the chimpanzee appears to be based on food resources that yield the maximum amount of nutrients. Such resources are generally widely dispersed and may also vary in temporal distribution from year to year. This explains the exceptional size of the range of the chimpanzee and its large "supplying area", compared to that of the other frugivorous primate species (Wrangham, this volume; Hladik, 1975). The feeding strategy of *Presbytis senex* (Hladik, this volume) is exactly the contrary of that of *Pan troglodytes*, with the utilization of common food sources associated with low costs in ranging and feeding movements and with low return in energy.

Feeding behaviour is conditioned by the long term response to the nutrients (see Hladik *et al.*, 1971a; Casimir, 1975; Hladik, this volume); but the chimpanzees selection of food must necessarily be based on the immediate effects of the soluble substances detected by taste. This is the only way to increase the efficiency of foraging and gathering in an animal looking for food species dispersed over a wide range. There is no evidence that all the important nutrients can be detected by taste but the secondary compounds can be associated with the long term response and provoke an immediate effect; this might be the reason why some substances (see Section 5.4) which have no obvious effect on nutrition are selected.

7. SUMMARY

1, 2. A field study of one year (1971–72) and three months (1975) was carried out on a population of chimpanzees reintroduced to the rain forest of Ipassa, near Makokou, Gabon. Quantitative data on the food ingested were collected. Results of this study are compared with data collected by R. W. Wrangham in the Gombe National Park, Tanzania. The number of plant species is greater in Gabon than at Gombe and the variety of food plants eaten is also greater.

3. In Gabon, as at Gombe, chimpanzees fed more on fruits in the first-half of the day and more on leaves in the second-half. During the rainy season, a marked peak in leaf eating occurred in the last two hours of activity.

Small differences in the feeding techniques and food choice appear between the chimpanzees in Gabon and at Gombe. "Fishing" concerns mainly termites at Gombe and ants in Gabon. *Macrotermes* are eaten at Gombe, not in Gabon. Bark is utilized as a fibre complement with animal food in Gabon, while at Gombe, leaves play this role.

4. Seasonal changes in diet were related to plant phenology and, as at Gombe, there are important differences between years. Ranging patterns are partly related to plant distributions (data from Gabon not sufficient for comparison).

The average annual food intake (fresh weight) was 68% fruits, 28% leaves and barks and stems, 4% animal food.

5. The composition of the food specimens collected in Gabon, show that the feeding strategy of the chimpanzee is based on the utilization of the dispersed resources yielding the maximum amount of nutrients. The low protein content of fruits is compensated for by the high content of young leaves. Insects are selected for specific amino acids.

Minerals are mostly supplied by different food plants and geophagy is not an adaptation to dietetic balancing. The earth ingested may serve to adsorb tannins or other secondary compounds.

Some rare plants showing high levels of toxic compounds are avoided by chimpanzees. Although "secondary compounds" are found in small amounts in many food plants, there is no evidence that chimpanzees select plant species where these are absent.

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